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VOL. 54 DECEMBER, 1927 No. 9

JAN 24 1928

BULLETIN

OF THE

TORREY BOTANICAL CLUB

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PUBLISHED FOR THE CLUB

PRESS OF
THE INTELLIGENCER PRINTING COMPANY
8 W. KING ST., LANCASTER, PA.

Entered at the Post Office at Lancaster, Pa., as second class matter.

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Soil temperatures in redwood and hemlock forests

FORREST SHREVE

During the latter part of the summer of 1925 an investigation was made of the soil temperature conditions within and just outside an area of redwood forest in the Santa Lucia Mountains, California. Readings were secured under natural conditions, under conditions of removal of litter of leaves in the forest, and also under conditions produced by using the forest litter as a cover for bare ground in openings in the forest. The investigation of unforested areas included one near the forest, in the floor of a canyon, and one on the summit of an adjacent ridge. In the following winter the writer found that Mr. Freeman Weis, of the United States Department of Agriculture, had secured a series of soil temperature readings over nearly the same period in a mature stand of hemlock near Freeland, Pennsylvania. Mr. Weis very generously provided the writer with a copy of his data for comparison and publication. The present paper embodies the California data, the Pennsylvania data, and such comparison as is possible.

All of the figures presented were secured with the Friez thermograph, calibrated before and after use, and checked monthly during use. The means and extremes have been read from the thermograph slips. All data are given in Fahrenheit degrees. In the California series the data were secured at depths of 3 inches and 12 inches, in the Pennsylvania series only at 3 inches. Readings under natural conditions were taken with as little disturbance of the surface as possible. Removal of the natural litter in the redwood forest was done so as to take all loose leaves, and all blackened but loosely placed leaves. The level at which the remains of blackened leaves form a fairly compact layer was left undisturbed, and this level was in all cases used as the datum for setting the cylinder of the

[The BULLETIN for November (**54**: 603–648) was issued 5 December, 1927.]

thermograph at a given depth. The material used to form a mulch over the bare surface of the unforested area was the same as that removed in the forest. It was placed on the ground in as natural a manner as possible, to a depth of 5 inches, with the blackened material beneath, and freshly fallen twigs on top, the area covered being 100 square feet, with the thermograph bulb at the center.

The readings in redwood forest were taken in the floor of Rocky Creek canyon, 12 miles south of Carmel, California, and about one mile from the spot at which this stream debouches into the sea. The readings in the opening were taken about 600 feet from the forest station, in a spot bare of perennial vegetation and not shaded by trees between 8 a.m. and 5 p.m. There is no apparent reason why the opening should not form

TABLE I

Soil temperature at depth of 3 inches in hemlock forest near Freeland, Pennsylvania

WEEK ENDING —1925	MEAN		ABS.		WEEK ENDING	ABS.		WEEK ENDING	ABS.	
	max.	min.	max.	min.		max.	min.		max.	min.
May 23	45	43	46	41	July 4	52	48	Aug. 15	54	52
May 30	44	42	49	40	July 11	56	49	Aug. 22	55	51
June 6	50	47	53	44	July 18	55	50	Aug. 29	54	49
June 13	52	50	53	47	July 25	54	50	Sept. 5	53	49
June 20	52	50	54	49	Aug. 1	53	50	Sept. 12	56	51
June 27	—	—	51	48	Aug. 8	53	50	Sept. 19	57	51

a successful habitat for the redwood. The ridge readings were taken on Long Ridge, about 1200 feet above the elevation of the other stations, and about one-half mile distant. The ridge is without perennial vegetation at this spot and is covered during the summer with the inactive or dead grasses and herbaceous plants which appear during the spring rains. In this region redwood forest is never found occupying the summits of ridges, and only occasional groves of small, wind-blown trees are found on the upper slopes. A fuller description of the area investigated and of its vegetation has been published elsewhere.[1]

[1] Shreve, Forrest. The Vegetation of a Coastal Mountain Range. Ecology **8**: 27–44. *f. 1–6.* 1927. Shreve, Forrest. The Physical Conditions of a Coastal Mountain Range. Ecology **8**: 398–414. 1927.

The coastal redwood forests present ideal conditions for the maintenance of extremely uniform soil temperatures. Given the equable marine climate, the heavy shade of the great trees, and the depth of the litter with which the ground is covered, and the combined effect is a remarkably stabilizing one.

The readings taken by Mr. Weis at a depth of 3 inches in a mature stand of hemlock (*Tsuga canadensis*) near Freeland, Luzerne County, Pennsylvania, are shown in TABLE 1. The records extend from May 16 to September 19, 1925. The record is characterized throughout by an extremely small daily range. For the five weeks from May 16 to June 20 the mean

TABLE 2

Soil temperature at depth of 3 or 12 inches in redwood forest near Carmel, California, with and without natural mulch of leaves

CONDITION OF SURFACE	DEPTH	WEEK ENDING	AVERAGE		ABSOLUTE	
			max.	min.	max.	min.
Natural cover	3 in.	July 21, '25	59.1	56.5	60.0	55.6
" "	3 in.	July 28	59.0	57.5	59.9	56.9
" "	3 in.	Aug. 4	59.4	58.0	59.9	57.4
" "	3 in.	Aug. 11	59.4	57.4	60.0	57.0
" "	3 in.	Aug. 18	59.1	57.1	60.0	55.9
Natural cover removed	3 in.	Aug. 26	59.7	55.4	60.0	54.8
" " "	3 in.	Sept. 2	58.9	55.2	59.5	54.0
" " "	3 in.	Sept. 9	61.4	56.6	62.3	55.1
" " "	3 in.	Sept. 15	60.3	57.0	61.5	55.0
Natural cover	12 in.	Sept. 22	58.8	58.7	60.0	57.7
" "	12 in.	Sept. 29	58.3	57.9	59.0	57.0
" "	12 in.	Oct. 6	57.5	57.1	58.2	56.1
" "	12 in.	Oct. 13	57.3	56.9	57.8	56.8

weekly range was 2.2° for the soil, as compared with 15.0° for the air, and the absolute weekly range was 6.8°, as against 43° for the air. For the succeeding 13 weeks the absolute weekly range was 4.1°. The absolute weekly maximum temperature rose almost continuously from 46° in the week of May 16 to 56° in the week of July 11, and remained within 4° of the same value until the middle of September, reaching the highest value for the summer at 57° on the week ending September 19. The weekly absolute minimum for the entire record ranged from 40° to 52°, but during the principal part of the summer it varied only through a range of 4°. The weekly absolute maximum

temperatures of the air ranged from 66° to 82° for the period of the record, and the weekly absolute minimum temperature from 32° to 56°.

The readings taken in a virgin stand of redwood (*Sequoia sempervirens*) near Carmel, California, are shown in TABLE 2. Readings taken at 3 inches under the natural cover of fallen leaves were secured during the last two weeks of July and the first three weeks of August, and again at 12 inches during the last half of September and the first half of October. The highest maximum recorded at 3 inches was 60.0° and the lowest minimum was 55.6°. The average daily maximum for the five weeks was 59.2° and the average daily minimum 57.3°, giving a mean daily range of 1.9°. In order to compare the California and Pennsylvania records it is necessary to determine the average of the weekly absolute maximum and minimum for the five weeks in which the records were taken under comparable conditions. For the redwood forest the values are: average absolute maximum 60.0°, average absolute minimum 56.5°. The corresponding figures for the hemlock forest are 53.8° and 50.4°. The range between these rather awkward expressions of the extremes is 3.5° for the redwood forest and 3.4° for the hemlock. In short, the actual temperature at 3 inches under redwoods is about 6° higher than it is under hemlocks, growing 2500 miles distant, and the weekly range of temperature is virtually identical for the two forests.

After records had been secured at 3 inches in the redwood forest for five weeks, under normal conditions, the natural mulch of fallen twigs and leaves was removed to a depth of five inches without change in the thermograph. Records were secured for four weeks without the mulch. The average weekly maximum for the period, with normal cover, was 59.2, the average weekly minimum 57.3°. For the period with cover removed the same data were respectively 60.1° and 56.0°. The very slight difference due to removal of the mulch is in the expected direction of elevating the maximum and lowering the minimum. The difference is so small as to have little significance, however, even in a realm where small differences of temperature are more important than they are in the air.

The records secured at a depth of 12 inches under the natural mulch of leaves, over a period of four weeks, show little difference

from those taken at a depth of 3 inches. The graphs taken at the greater depth are very flat, the minimum for the day occurring at 1 to 2 p.m. and the maximum at about midnight. The average maximum was 1.2° lower than at 3 inches, and the average minimum 0.3° higher.

Records were taken in the opening in the redwood forest at 3 inches, with the natural nearly bare surface, for three weeks, and for the same period with a mulch of redwood leaves 5 inches thick. Records were also secured at 12 inches for two weeks with natural surface and for two weeks with the mulch

TABLE 3

Soil temperature at depth of 3 or 12 inches in open area in redwood forest near Carmel, California, without and with mulch of leaves from redwood forest

CONDITION OF SURFACE	DEPTH	WEEK ENDING	AVERAGE		ABSOLUTE	
			max.	min.	max.	min.
Natural bare state	3 in.	July 28, '25	77.5	64.3	81.5	61.0
" " "	3 in.	Aug. 4	82.3	67.8	85.0	66.5
Mulch of leaves on	3 in.	Aug. 18	70.8	66.9	74.0	65.0
Natural bare state	3 in.	Aug. 26	86.2	63.0	87.0	56.5
Mulch of leaves on	3 in.	Sept. 2	72.3	65.3	79.1	64.0
" " " "	3 in.	Sept. 9	70.3	64.0	71.4	62.0
Natural bare state	12 in.	Sept. 22	66.0	63.4	67.9	62.0
" " "	12 in.	Sept. 29	66.1	63.8	66.5	63.2
Mulch on leaves on	12 in.	Oct. 6	61.8	60.3	64.1	59.1
" " " "	12 in.	Oct. 13	59.6	58.8	60.3	57.6
Average 3 wks. without mulch, at 3 in.			82.0	65.0	84.5	61.3
Average 3 wks. with mulch at 3 in.			71.1	65.4	74.8	63.7
Average 2 wks. without mulch, at 12 in.			66.1	63.6	67.2	62.6
Average 2 wks. with mulch, at 12 in.			60.7	59.5	62.2	58.3

of leaves. The resulting data are given in TABLE 3, together with the average weekly maximum and minimum under the four sets of conditions. At 3 inches the effect of the leaf mulch was to lower the average maximum 10.9°, while the average minimum remained nearly the same. At 12 inches the average maximum was lowered 5.4°, and the average minimum was also lowered 4.1°. It is to be expected that protection from active nocturnal radiation provided by the mulch would cause a higher minimum at a slight depth. At 12 inches, however, a depth at which the effect of radiation is not strongly exerted, the mini-

mum is lowered on account of the very much lower range of temperature of the superficial layers of soil during the day.

It is of interest to compare the temperatures in the forest with those in the opening, as taken under the natural conditions of the two localities. Considering the 3 inch data for the 2 weeks ending July 28, and August 4, the average maximum in the forest was 59.2° and in the opening 79.9°, while the average minimum was 57.7° in the forest and 66.0° in the opening. A difference of 20.7° in the maxima and 8.3° minima is indicated. A range of 1.5° in the forest is contrasted with one of 13.9° in the opening. At the 12 inch depth the average maximum in the forest was 58.6° and in the opening 66.0°, the average minima

TABLE 4

Soil temperature at depth of 3 or 12 inches in open grass on ridge overlooking redwood forest, near Carmel, California

CONDITION OF SURFACE	DEPTH	WEEK ENDING	AVERAGE		ABSOLUTE	
			max.	min.	max.	min.
Natural cover	3 in.	Aug. 4, '25	95.1	73.9	99.9	72.9
" "	3 in.	Aug. 11	94.4	74.4	98.0	71.9
" "	3 in.	Sept. 2	93.0	72.5	97.9	70.0
" "	3 in.	Sept. 9	87.5	68.2	93.0	64.0
" "	3 in.	Sept. 15	78.4	62.4	84.0	58.6
" "	12 in.	Sept. 22	71.6	70.7	72.1	70.0
" "	12 in.	Sept. 29	72.9	71.7	73.0	71.1
" "	12 in.	Oct. 6	70.6	69.8	71.6	69.0
" "	12 in.	Oct. 13	67.7	66.9	70.0	63.2
Average, 5 weeks at 3 in.			89.7	70.3	94.6	67.5
Average, 4 weeks at 12 in.			70.7	69.8	71.7	68.3

were respectively 58.3° and 63.6°. At this depth there is a smaller difference between the maxima, 7.4°, and the minima, 4.9°.

Since the difference between the average maxima at 3 inches in forest and opening is 20.7° and the difference between the maxima in the open with and without mulch is 10.9°, it appears that a 5 inch mulch of leaves will bring the maximum soil temperature of an opening half way back to the temperature of the forest soil.

The readings taken on an open ridge are shown in TABLE 4, covering five weeks at 3 inches and four weeks at 12 inches.

Owing to accidental failure to secure a continuous series of records, there is only one week in which the ridge record and that in the opening were taken simultaneously. During the five weeks from July 28 to September 15 the average maximum on the ridge was 89.7° and the average minimum 70.3°. This maximum is 7.7° higher than the average for three weeks in the opening, although in the simultaneous records of the week ending August 4 the average maximum for the ridge was 12.8° above that for the opening, and 35.7° above that for the redwood forest. The average minimum for the week ending August 4 was 6.6° higher on the ridge than in the opening, and 16.4° higher on the ridge than in the forest. With respect to the temperature at 12 inches the average maxima for the two weeks ending September 22 and 29 were 72.2° for the ridge, 66.0° for the opening, and 58.5° for the forest. The average minima for the same stations for the same period are respectively 71.2°, 63.6°, and 58.3°.

The establishment of a forest in an unforested locality requires the existence of an initial set of conditions favorable to seedling trees. During the course of its growth and development a newly established forest will modify many of the environmental conditions in such a direction as to make them more favorable for the adult trees of the mature forest. This reciprocal effect of vegetation upon its own environment is, of course, true of any of the closed types of vegetation. High temperature of the soil is one of the unfavorable conditions encountered in the spread of redwood forest onto new ground within its distributional area. Under natural conditions the forest spreads only by invasion of other established communities in which the conditions have already been ameliorated to a great extent. In any efforts at reforestation with redwood it will be necessary to provide some natural or artificial set of ameliorating agencies. The difference that has been shown to exist between the soil temperatures in the forest and in a nearby opening may well be a critical one for young redwoods. The conditions which result in high soil temperatures and a greater daily range are also the ones that favor rapid drying of the soil and other features hostile to the success of seedling trees.

The differences between the temperatures in the opening and on the ridge, one-half mile distant and 1200 feet higher, are due

to a series of topographic and climatic conditions on which the vegetation has had extremely little influence in either locality. There is no reason to believe that the soil temperature conditions of the opening could not be made to correspond to those of the forest if such conditions came about as to make possible the gradual steps for development of the forest at that place. It has been shown that a mulch of leaves and twigs, closely similar to that which covers the floor of the forest, will do much to bring the soil temperatures of the opening down toward those of the forest. If heavy shade were added to the mulch the change would doubtless be nearly complete. It remains very doubtful whether the ameliorating effects of the forest cover could be initiated and carried on, in this region, far enough to bring the conditions of the ridge within the range of possible soil temperatures for the growth of the redwood. Even mulch and shade would doubtless fail to reduce the maxima of the late summer to any such extent as 35.7°, the amount by which the ridge and forest maxima have been shown to differ.

Much careful work will be required on the optimum and limiting temperatures for growth of redwood roots before we are in a position to use soil temperature data, in conjunction with others, in determining the advisability of efforts toward reforestation or afforestation in a given locality.

THE DESERT LABORATORY,
TUCSON, ARIZONA

A cytological and a genetical study of Petunia—I

MARGARET C. FERGUSON

(WITH A TEXT FIGURE AND PLATES 35, 36)

INTRODUCTION

Since the fall of 1919 the genus *Petunia* has been continuously studied at Wellesley College by the undergraduate students in the regular course in Cytology and Genetics, by several candidates for the M.A. degree and by the writer.

Preliminary studies were made on seven cultivated strains and two wild species. From these, four forms were selected for more intensive study. These include three cultivated strains and one natural species—population 6, white; population 8, very deep purple; population 13, pink; and *Petunia nyctaginiflora* Juss., population 14, white. The seeds of the last named species were sent to us by Professor L. R. Parodi of the University of Buenos Aires, South America. There has not been the slightest suggestion of impurity, as regards color or shape of flower, either in the plants grown directly from this seed or in subsequent generations. Professor Parodi also very kindly sent us seed of the supposedly wild *P. violacea* Lind., but the plants grown from this seed showed marked variability in flower color. This seed may have been the result of crossing in nature. But we had no way of determining the earlier genetical history of this strain and, as it very evidently was not a pure form of *P. violacea* Lind., this population was discarded.

In our efforts to secure wild species of *Petunia*, we have corresponded with a number of botanists who were travelling in South America, with government officials, and with botanic gardens and seed houses in four different countries. As yet *P. nyctaginiflora* Juss. is the only natural species which we have succeeded in obtaining. Dr. Arthur W. Hill, F. R. S., Director of the Royal Botanic Gardens at Kew, England, has twice most kindly sent us plants of *P. violacea* Lind., but after the delay necessitated by government inspection at Washington, no single one of these plants has reached Wellesley alive.

By all tests available three of the four forms which we have under consideration are now homozygous for both flower color and shape of flower. The fourth form, population 13, pink, always gives some flowers, as the plants age, that are more or less flecked or spotted with white; but neither in back crosses nor in selfings for several generations has it shown any other color than the pink of the original stock.

Petunia is readily propagated by cuttings. We have, therefore, been able to have several generations of a given population under observation at the same time. Since seeds sown out of doors during the last of May give plants which are in blossom before the middle of August, it was assumed that we could secure three or four generations from seed in a given year. However, this has not been found possible. There is very little bloom from October first to December first and full blossoming vigor is not displayed before the last of February or the first of March. It has been possible to overcome somewhat the paucity of blossoms during the late fall and winter by the installation of 1000-watt, type C lamps with special reflectors in one of the 'petunia houses.' But there is also a marked seasonal sterility, so that few viable seeds are set during the period when flowers are rare. It is not our purpose to discuss at this time the phenomena of sterility or seed germination. These and other problems in the life history of *Petunia* will form the bases of later papers. To date about 25,000 plants have been grown and observed, and more than 4,000 slides of serial sections studied.

AN UNRECORDED METHOD OF 'DOUBLE FERTILIZATION'[1]

The structure of the mature embryo-sac in *Petunia* conforms very closely to the type ordinarily described for Angiosperms (PLATE 35, FIG. 1). As a rule the polar nuclei have fused before the pollen tube enters the sac, but fusion may be delayed until the growing male gametophyte has penetrated the wall of the embryo sac and extended to or beyond the egg nucleus (FIGS. 2, 3). The tip of the pollen tube reaches this position in the sac from 72 to 96 hours after pollination. When the tip of the tube has reached the level of the egg nucleus or thereabouts, but

[1] Presented before the Botanical Society of America at the Washington meeting in December, 1924.

before either sperm nucleus has been discharged from it, the endosperm nucleus divides (FIG. 4). At the close of this division a delicate wall is laid down, dividing the sac into a large basal cell and a smaller micropylar one (FIG. 5). In 1902 Guignard[1] described the early stages in the development of the endosperm in *Nicotiana* and *Datura*. He found, in both these genera, that in endosperm formation nuclear division is followed by cell division, and he concluded that in the Solanaceae there is no early free-nucleated stage in the development of the endosperm. *Petunia* is now found to be in full agreement with this generalization for the Solanaceae. Guignard's figure 43, showing the structure of an embryo sac in *Datura laevis* at the close of the first division of the endosperm, is, with the exception of the relative sizes of the two endosperm cells, practically identical with figure 5 of this paper. This figure of Guignard's is reproduced by Coulter and Chamberlain,[2] page 165. According to Guignard's interpretation, this first division of the endosperm does not occur until after 'triple fusion' and fertilization. In *Petunia*, it has been possible to demonstrate beyond question, as will appear later, that the primary division of the endosperm is completed before the sperm nuclei leave the pollen tube. It is generally stated that the sperm gives the necessary impulse for further cell division. In this case it would appear that the presence of the swollen tip of the pollen tube within the sac is sufficient stimulation to incite the development of the endosperm. In the thousands of ovules studied, no endosperm cells have ever been observed in an embryo sac prior to the entrance of the pollen tube; and in no case has a sperm nucleus been found outside the pollen tube before the division of the primary endosperm cell.

The sequence of events immediately following the division of the endosperm into two cells is not always the same. Before further mitoses take place in the endosperm, the lower sperm nucleus may escape from the tip of the tube and associate itself with the nucleus of the primary, micropylar, endosperm cell (FIGS. 6–8). At other times, before the liberation of the sperm

[1] Guignard, L. La double fécondation chez les Solanées. Jour. Botanique **16**: 145–167. *f. 1–45*. 1902.

[2] Coulter, J. M., and Chamberlain, C. J. Morphology of Angiosperms. New York. 1903.

nucleus from the pollen tube, the primary, basal, endosperm cell divides, forming a large basal cell and a much smaller upper cell. The wall separating these two cells runs parallel with the first wall laid down (FIG. 9). And in many cases, while both sperm nuclei are still within the tube, the larger, lower cell, formed as the result of the second mitosis, divides (FIG. 10). The resulting two cells are nearly equal in size, and the wall between them lies practically parallel to the two cross walls earlier formed (FIG. 11). In all cases, when the micropylar 'fusion-nucleus' is fully established or is in the early prophase of division, the endosperm consists of a tier of four cells. The uppermost cell, the primary, micropylar, endosperm cell, is always smaller than the others. The three cells below it are descendants of the primary basal cell formed at the close of the first endosperm division (FIGS. 11, 12).

The life history of the male gametophyte will be discussed in a later paper. At present I wish merely to call attention to the fact that the lower male nucleus as it lies in the tip of the tube is more or less crescent or banana shaped, though often appearing elliptical because of the view presented. It is very dense, showing little or no structure, and takes stains with great avidity (FIGS. 17a–e). As it leaves the tube and comes in contact with the upper endosperm nucleus, it increases somewhat in size (FIG. 18). There is no evidence that it enters the endosperm nucleus, but as the two press closely together, it increases in size, loses its dense appearance, and displays a more or less completely reticulated structure inclosing a comparatively large nucleolus (FIG. 19). At this stage it resembles very closely, to all appearances, the larger endosperm nucleus, with which it later becomes so closely associated that the resulting nucleus gives no structural suggestion of its dual nature (FIGS. 11, 20).

When the upper endosperm cell with its 'fusion-nucleus' divides, the wall is laid down at right angles to the walls previously formed within the embryo sac. The ensuing divisions proceed with remarkable regularity, as do the earlier divisions within the sac, and in both cases the first division is at the micropylar end, and each succeeding division occurs in the adjacent basal cell. While there may be an overlapping in the mitoses within the first four cells of the endosperm, the lower

cell beginning to divide before the adjacent upper cell has fully completed its division, I have never found the four cells dividing simultaneously as shown in Guignard's figure 45 (*op. cit.*). In some hundred or more cases studied I have never found an exception, in early endosperm formation, to the series of steps shown in the accompanying diagram (TEXT FIG. 1)

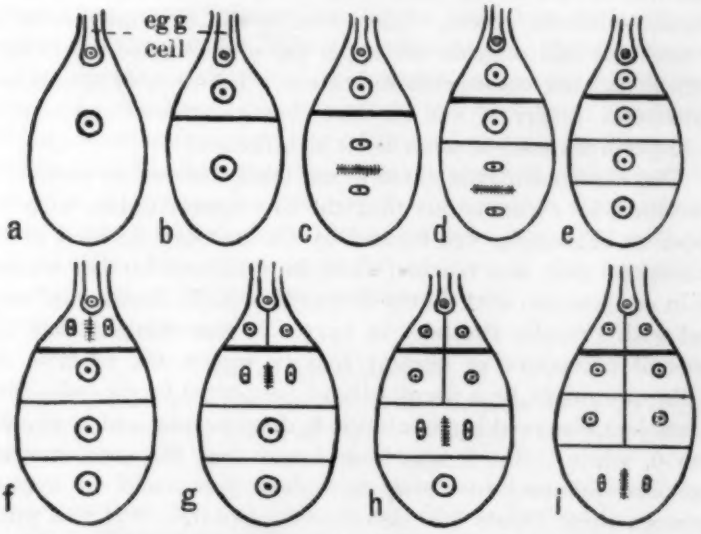

FIG. 1. Diagrammatic presentation of the steps in early endosperm formation in *Petunia*.

although, as stated above, the divisions may overlap somewhat. It will be noted (*b–e*) that each new division is in the basal cell formed by the preceding division. When anticlinal walls are laid down, they also begin at the micropylar end and move in regular succession to the base (*f–i*). Immediately following these divisions, or synchronous with them, anticlinal walls are laid down, which lie at right angles to both the horizontal walls and the longitudinal walls shown in the diagram above. Thus each of the four layers of endosperm cells is divided into four cells or quadrants (FIGS. 13, 14). Twelve of the cells resulting are the descendants of the primary, basal, endosperm cell and four are derived from the primary, micropylar, endosperm cell after its union with a sperm nucleus.

When the early steps in this process were first observed as in figures 4 to 7, it was assumed that the lower or basal endosperm cell would disintegrate early, and that the functional endosperm would be formed from the upper or micropylar cell. But such did not prove to be the case. On the contrary, at the 16-cell stage three fourths of the endosperm is derived from the cell that was cut off at the time of its inception from any intimate relation with the sperm. Later studies will determine whether or not from this stage on the upper tier of cells gains the ascendency in further endosperm formation. If fusion of sperm and endosperm nuclei is not an incentive to greater activity in endosperm formation, what is its significance?

The conclusion that there is no 'triple fusion,' as ordinarily described, in *Petunia*, but that the first sperm unites with the upper or micropylar cell formed by the primary division of the endosperm cell, was reached early in 1921 and further worked on in conjunction with Betty Watt (Mrs. S. T. Brooks) in 1923, and with Priscilla Presbrey in 1925. It was thought that this unusual procedure in nuclear fusions within the embryo sac of *Petunia* might be a peculiarity of cultivated forms only, since it was first observed in population 8, deep purple, and in population 6, white. But it was later found that the same method was also followed in *P. nyctaginiflora* Juss., and in hybrids between these plants (see description of plates). If this interpretation regarding nuclear fusions within the embryo sac be correct, it should easily be checked up by chromosome counts. This, however, did not prove to be so simple a matter, for while mitotic figures are frequently observed in the endosperm, they have rarely been found in stages favorable for counting chromosomes with absolute certainty. Publication has been deferred until division stages clearly revealing chromosome number at the two critical points should be observed. Figure 15 leaves no doubt as to the number of chromosomes. Fourteen chromosomes are clearly shown, so arranged as to, at least, suggest two groups of seven each. This represents a cross section of a spindle just as the chromosomes are assembling to form the equatorial plate stage in the second division of the basal endosperm cell. This mitotic figure has practically the same position in the embryo sac as has the spindle shown in figure 10.

In figure 16 the chromosomes are found more closely massed

than in figure 15, but still there can be no doubt that there are 21 chromosomes present. This is the figure presented by a dividing nucleus in the primary, micropylar, endosperm cell which has virtually the same position in the embryo sac as the slightly earlier stage shown in figure 12. Since the x number of chromosomes in *Petunia* is seven, and the nuclei derived from the primary, *basal*, endosperm cell carry double that number rather than $3x$, it follows that 'triple fusion' as ordinarily described does not occur. On the other hand, the first division of the primary, *micropylar*, endosperm cell shows 21 chromosomes, the number to be expected if the uppermost endosperm nucleus fused with a sperm or other nucleus. These facts as to chromosome number, together with the series of events outlined earlier in this paper, lead to no other conclusion than that the sperm nucleus first to leave the pollen tube fuses, not with the polar nuclei, but rather with the nucleus of the micropylar daughter cell of the primary endosperm cell.

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Description of plates 35, 36

All the figures have been reduced one-half from the size of the original drawings, so that the present magnification of figures 1–9 is approximately 600 diameters.

FIG. 1. Mature embryo sac. *a* = remnants of antipodals. *Petunia nyctaginiflora* Juss. Pop. 14. Slide made by Priscilla Presbrey.

FIG. 2. Embryo sac showing tip of pollen tube at base of egg, the polar nuclei not fully united and one antipodal nucleus still intact. *d* = nucleus of synergid. *c* = chromidia or other deeply staining material in the pollen tube. *s. n.* = sperm nuclei. Pop. 8, 85 hours after pollination.

FIG. 3. Embryo sac showing tip of pollen tube at base of egg and endosperm nucleus fully established. No trace of polars to be found. Pop. 14, 80 hours after pollination. Slide made by Hannah Adams.

FIG. 4. Micropylar end of embryo sac. Both sperm nuclei still within the pollen tube and primary endosperm nucleus in telophase of division. Pop. 14, 90 hours after pollination. Slide made by Priscilla Presbrey.

FIG. 5. Embryo sac after first division of endosperm. The micropylar endosperm cell smaller than the basal. The two sperm nuclei still within the pollen tube. Pop. 14. Slide made by Gertrude McDiarmid.

FIG. 6. Embryo sac with two-celled endosperm, showing the lower sperm nucleus just escaped from the pollen tube. Pop. 6, 96 hours after pollination.

FIG. 7. Embryo sac with two-celled endosperm. One sperm nucleus still within the tube, the other in contact with the nucleus of the micropylar endosperm cell. *d* = nucleus of synergid. *e. n.* = egg nucleus. Pop. 8, 96 hours after pollination.

FIG. 8. Embryo sac with two-celled endosperm, the basal cell in division. The lower sperm nucleus has just come in contact with the nucleus of the micropylar endosperm cell. *d* = nucleus of synergid. F_1 of Pop. 8 × Pop. 6, 100 hours after pollination.

FIG. 9. An embryo sac with three endosperm cells. The two sperm nuclei still within the tube. *b* = disintegrating nucellar tissue. F_1 of Pop. 14 × Pop. 8, 112 hours after pollination. Material put up by Gertrude Seelye.

Plate 36

FIG. 10. Embryo sac with three endosperm cells, the basal one in division. Sperm nuclei still in tube, the lower one about to escape. × 600. *e. n.* = egg nucleus. 124 hours after pollination.

FIG. 11. Embryo sac with three endosperm cells derived from the primary, basal, endosperm cell. The primary, micropylar, endosperm cell has not divided but its nucleus and the lower sperm nucleus have united to form the one large 'fusion-nucleus.' The second sperm nucleus still within the tube. × 600. *b* = disintegrating nucellar tissue. Pop. 8, 120 hours after pollination. Slide made by Louise Hall.

FIG. 12. A typical embryo sac at the time when the 'fusion-nucleus' of the primary, micropylar, endosperm cell divides. One sperm still within the pollen tube. × 600. F_1 of Pop. 14 × Pop. 8, 120 hours after pollination.

FIG. 13. The upper portion of an embryo sac after perpendicular or longitudinal walls have been formed in the primary, micropylar, endosperm cell and in the uppermost cell derived from the basal, primary, endosperm cell. × 600. Pop. 14, 120 hours after pollination. Slide made by Phyllis Albert.

FIG. 14. Cross section of an embryo sac after each of the four original endosperm cells have been divided into quadrants. × 280. F_1 of Pop. 14 × Pop. 8, 144 hours after pollination. Slide made by Dorothy Hammond.

FIG. 15. A late prophase in the division of the lower cell resulting from the division of the primary, basal, endosperm cell. Its position is similar to that of the division figure shown in figure 10. 14 chromosomes are shown, in two groups of 7 each. × 2000. Pop. 14, 96 hours after pollination. Slide made by Rachel Schreiner.

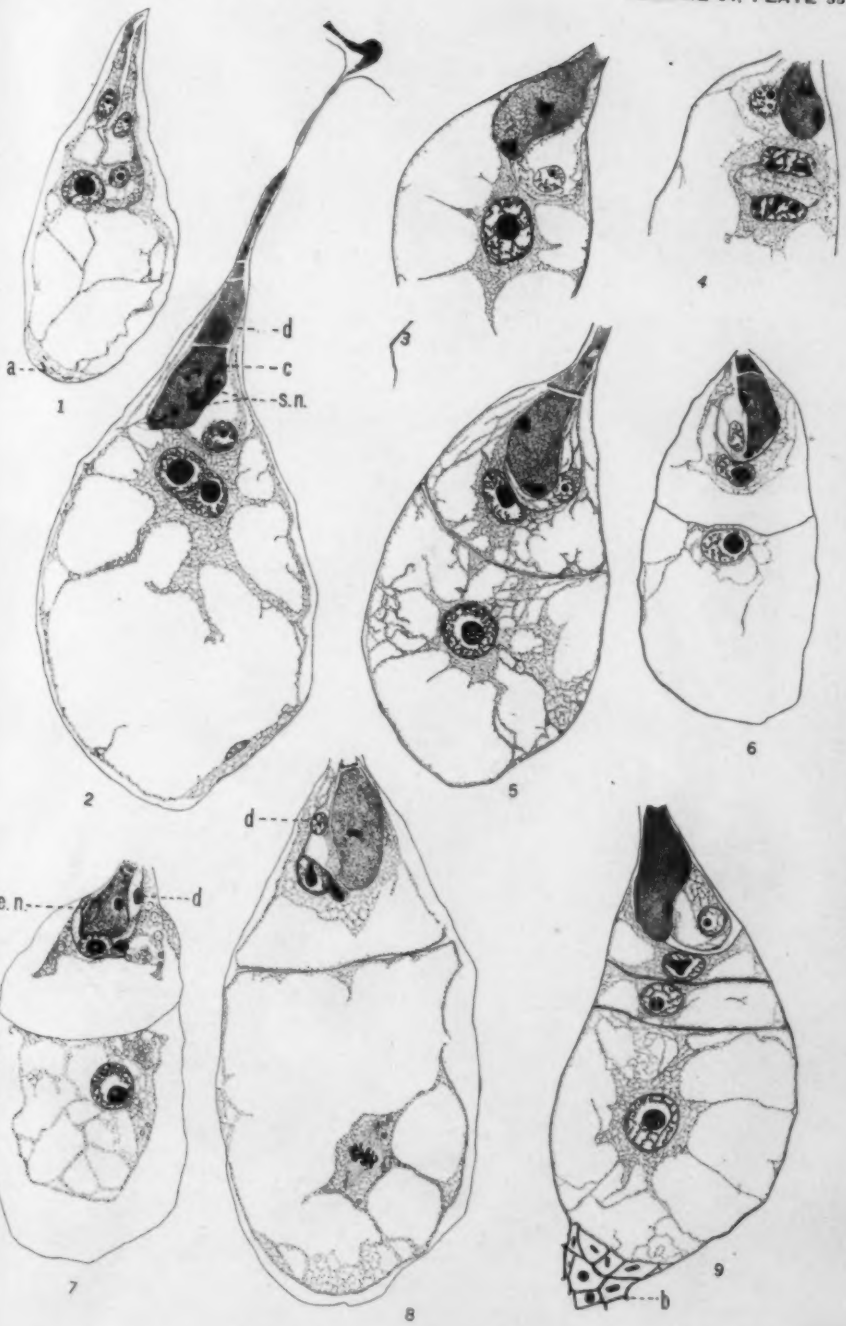
FIG. 16. Late prophase in the division of the 'fusion-nucleus' in the primary, micropylar, endosperm cell. Position of the mitotic figure is similar to the earlier stage shown in figure 12. 21 chromosomes are present. × 2000. F_1 of Pop. 14 × Pop. 8, 120 hours after pollination. Slide made by Marion Hunsicker.

FIG. 17, *a–e*. Various aspects of the sperm nucleus when in the tip of the pollen tube after its entrance into the embryo sac. × 2000. 90–96 hours after pollination. 17*a* = F_1 of Pop. 14 × Pop. 8. Slide made by Priscilla Presbrey. 17*b–e* = Pop. 5. Slide made by Dorothy Butler.

FIG. 18. A coiled sperm nucleus in contact with the nucleus of the primary, micropylar, endosperm cell. × 2000. Pop. 5, 96 hours after pollination. Slide made by Dorothy Butler.

FIG. 19. A later stage in the union of the sperm nucleus with the nucleus of the uppermost endosperm cell. ×1000. Pop. 6, 144 hours after pollination.

FIG. 20. The 'fusion-nucleus' in the primary, micropylar, endosperm cell. × 1000. Slide made by Miriam Schmaltz.



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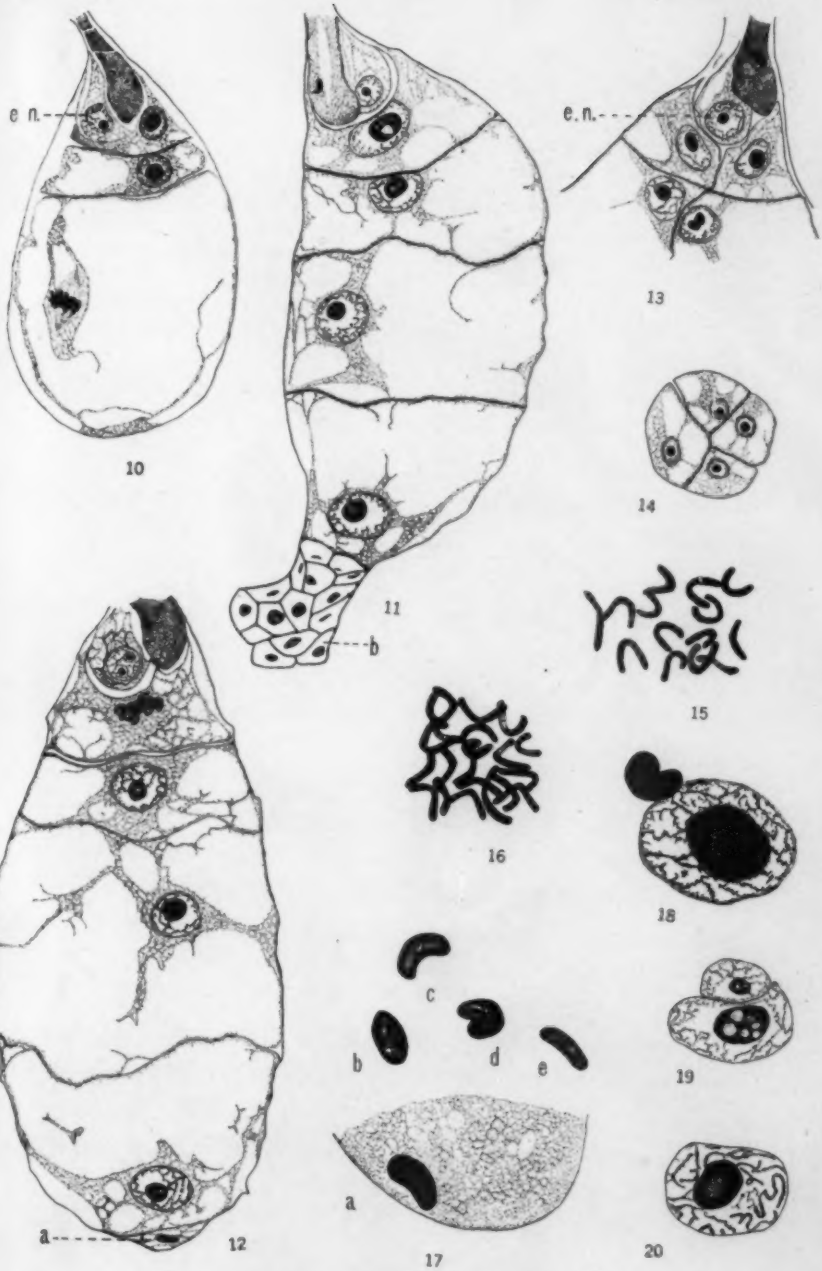

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INDEX TO AMERICAN BOTANICAL LITERATURE
1926–1927

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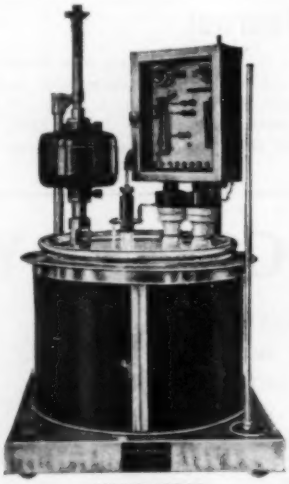

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